AN UNUSUAL BENNETTITALEAN LEAF FROM THE UPPER TRIASSIC OF THE SOUTH-WESTERN UNITED STATES

by SIDNEY R. ASH

ABSTRACT. *Eoginkgoites davidsonii* sp. nov. is a large pinnately compound bennettitalean leaf which has wedge-shaped pinnae. It is unusual because the pinnae are aggregated near the top of a short rachis and not arranged laterally on a long rachis as in other pinnate bennettitalean leaves. The veins radiate from the base of each pinna and divide and anastomose several times before reaching the margins and apices. The cuticle of the new species shows paracytic (syndetocheilic) stomata. Typically *E. davidsonii* sp. nov. is larger than the other species of the genus. *E. davidsonii* sp. nov. occurs at seven localities in the basal strata of the Upper Triassic Chinle Formation in Arizona and southern Utah and appears to be confined to the lowest unit (Shinarump Member) of the formation.

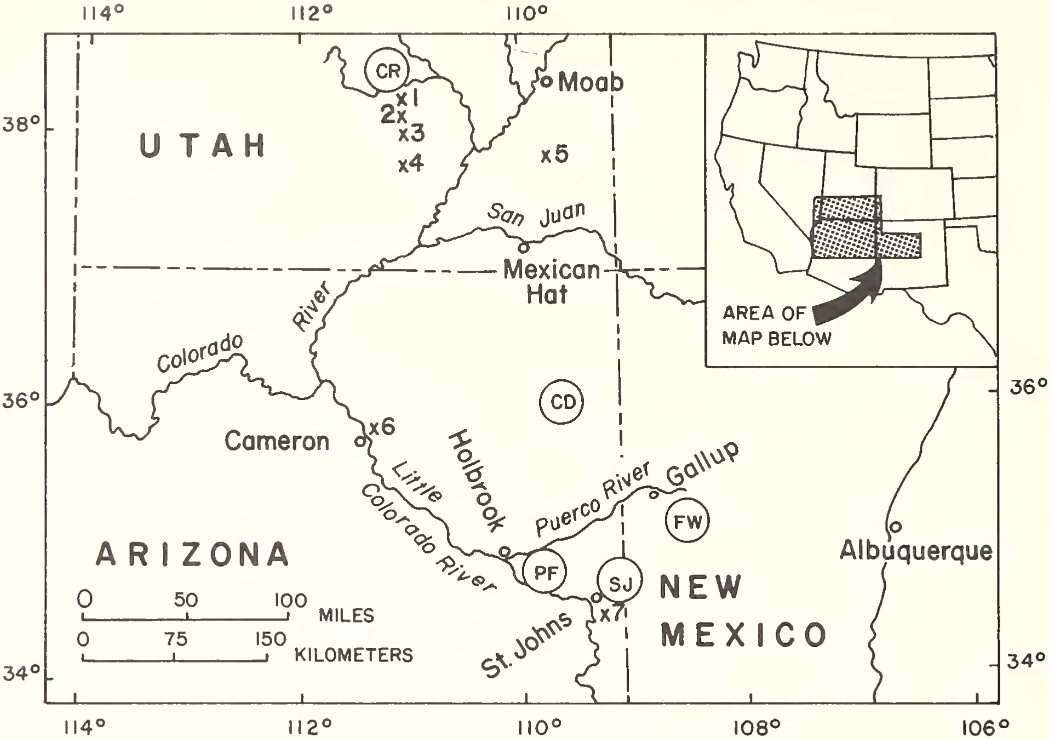
ANOTHER one of the unusual plant fossils that occur in the Upper Triassic rocks of the south-western United States is described in this report. However, unlike the others (e.g. *Sanmiguelia* Brown, 1956, *Dinophyton* Ash, 1970, and *Dechellyia* Ash, 1972), the relationships of this fossil are reasonably certain.

The fossil described here is a large pinnately compound leaf which has wedge-shaped pinnae. It has paracytic (syndetochelic) stomata so the fossil is assigned to the bennettitales. The leaf is unusual because the pinnae are aggregated near the top of a short rachis instead of being arranged laterally on a long rachis as in other pinnate bennettitalean leaves.

The remains of the leaf described here were first discovered during the early 1950s by field parties of the U.S. Geological Survey who were investigating the occurrence of uranium in the South-west. Those geologists found the leaf at four localities in the basal beds of the Upper Triassic Chinle Formation in Utah and Arizona (localities 1, 3, 6, 7 on text-figs. 1-3). Brown (*in* Davidson 1967; Smith *et al.* 1963; and Stewart *et al.* 1972) identified the fossil as the remains of the pinnate bennettitalean leaf *Sphenozamites rogersianus* Fontaine. During the past several years I also found the same leaf in the Chinle at other places (localities 2, 4, 5) in Utah and Arizona. Some of the specimens I collected were more complete than those examined by Brown and after study it became evident that the leaf is not related to *S. rogersianus.* Instead it is probably congeneric with *Eoginkgoites* Bock, 1952 from the Upper Triassic Newark Group of Pennsylvania as they both have the same shape and venation. Although Bock had attributed *Eoginkgoites* to the Ginkgoales cuticular studies of the Chinle, specimens showed that the genus actually is bennettitalean. Subsequently *Eoginkgoites* was redescribed and transferred to the Bennettitales (Ash 1976).

All the fossils attributed to *Eoginkgoites* are similar in architecture and venation. The fossils from Pennsylvania, however, are the remains of leaves that typically are smaller than those found in the south-western United States. Also the proportions of the pinnae are different, those from Pennsylvania being much narrower for their

[Palaeontology, Vol. 20, Part 3, 1977, pp. 641-659, pls. 77-79.]



TEXT-FIG. 1. Index map showing by numbers the localities that have yielded *Eoginkgoites davidsonii* sp. nov. (See the text for a description.) Other significant fossil-plant localities in the Chinle Formation are shown by encircled letters. They are CR, Capitol Reef National Park, Utah; FW, Fort Wingate, New Mexico; PF, Petrified Forest National Park, Arizona; SJ, St. Johns, Arizona, The same localities and symbols are used on text-figs. 2 and 3.

length than those from the South-west. Therefore, I believe that the fossils attributed to *Eoginkgoites* from the South-west should go into a new species which is described in this paper as *E. davidsonii* sp. nov.

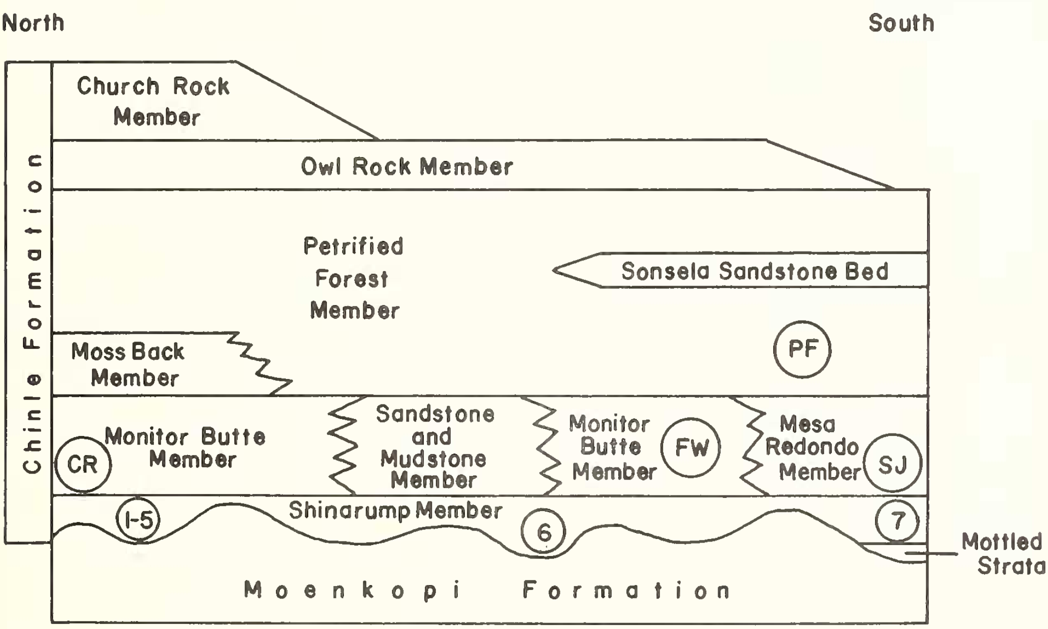
The abbreviations listed below are used in text-fig. 6 and Plates 77–79. They are the same as those used by Harris (1932*b*) in his study of cycadophyte stomata: d—dorsal guard cell cuticle; e—epistomatal pit; f—free edge of dorsal guard cell cuticle; g—guard cell; i—inner end of aperture tube; l—line of attachment of cuticle of subsidiary cell; o—outer end of aperture tube; oe—opening into epidermal cell papilla; os—opening into subsidiary cell papilla; p—polar region of guard cell; s—stomatal pore; su—subsidiary cell; w—wall separating guard cells.

GEOLOGIC SETTING

The Chinle Formation, which contains the new species of *Eoginkgoites*, is widely exposed in the south-western United States and ranges from 0 to about 450 m in thickness. It consists principally of structureless claystone although it also contains significant amounts of conglomerate, sandstone, siltstone, and mudstone. Locally the formation also contains thin interbeds of coaly material. The formation was deposited in a large inland basin by streams and in lakes and swamps during Late Triassic time. As a consequence of its environment of deposition the formation consists of several discontinuous lithologic units that often interfinger and intergrade along their boundaries. Various aspects of the complex stratigraphy of the Chinle have been discussed in a number of publications since the formation was first described by Gregory (1916). The most comprehensive modern discussion is in the report prepared by Stewart *et al.* (1972). Text-fig. 2 summarizes the nomenclature usually applied to the units recognized in the Chinle Formation in southern Utah and Arizona where the new species occurs. The text-figure also shows the stratigraphic position of the localities that contain *Eoginkgoites* sp. nov. and of the other important Chinle plant localities in the area.

The Chinle contains many plant and animal fossils. A summary of the fossils that have been found in the Chinle is contained in a recent symposium (C. S. and W. J. Breed 1972). One of the papers (Ash 1972) in that symposium showed that nearly all the plant megafossils described from the Chinle occur in the lower part of the formation in the Monitor Butte and Petrified Forest Members (see text-fig. 2). The new species, however, occurs only within the lower 12 m of the Chinle in the Shinarump Member.

The Shinarump Member typically is the lowest unit in the Chinle Formation. In places, such as locality 7, it is underlain by a thin sequence of rocks which are termed 'mottled strata'. These may represent a soil that developed before the Shinarump



TEXT-FIG. 2. Diagram showing the relationships of the various members of the Chinle in parts of Utah and Arizona. The diagram shows by numbers the approximate stratigraphic position of the localities that have yielded *Eoginkgoites davidsonii* sp. nov. It also shows by encircled letters the position of other significant fossil-plant localities in the Chinle.

was deposited in the area (Stewart *et al.* 1972). In most parts of the South-west the Shinarump or 'mottled strata' rest uncomformably on the underlying Moenkopi Formation of Early and Middle (?) Triassic age. As shown in text-fig. 2 the Shinarump is overlain by various members of the Chinle depending upon the area. The Shinarump averages about 9 m in thickness, but locally may be as much as 75 m thick where it fills channels. In some areas the Shinarump is only a few metres thick and in others it is entirely absent. The member is composed principally of cross-bedded conglomerate and conglomeratic sandstone, but at some places it also contains lenses and discontinuous beds of finer-grained rocks such as mudstone and siltstone and even carbonaceous layers and lenses of coaly material. Most of the unit is cross-stratified but horizontally bedded and massive strata also occur. Petrified wood and leaf impressions and compressions are locally abundant in the Shinarump (Ash 1975*a*, *b*).

The presence of cross-bedding, scour surfaces, and layers of conglomerate suggest that the Shinarump is principally a stream deposit. It is also suggested by the common occurrence in the member of plant debris such as large logs and local occurrence of continental vertebrate remains (Stewart *et al.* 1972). The fine-grained carbonaceous deposits and coal that occur in the Shinarump at places, however, probably represent either swamps that occurred along the margins of streams or that formed in abandoned stream channels. Certainly they do not represent high-energy deposits of the central part of streams.

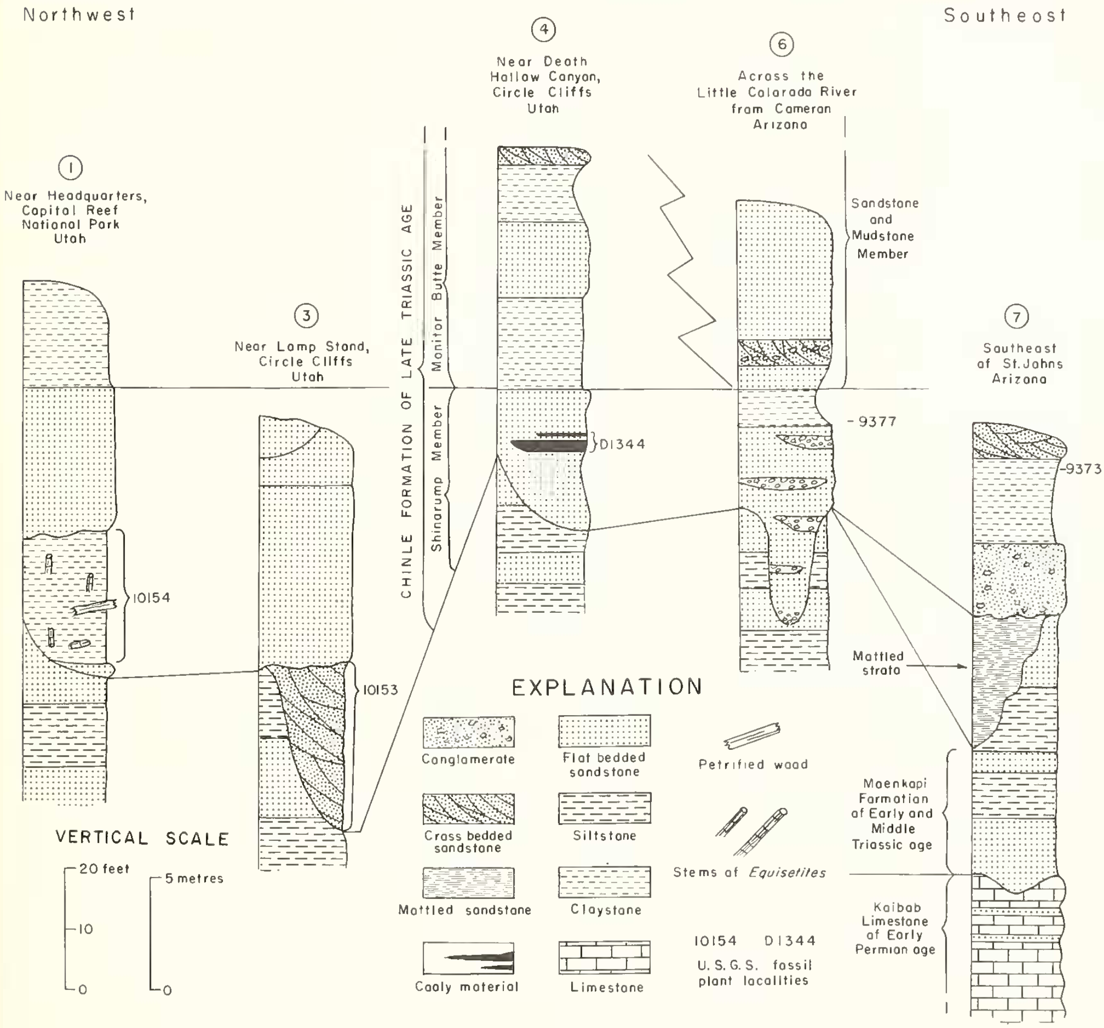
LOCALITIES

The seven localities which contain *E. davidsonii* sp. nov. extend from south-central Utah to east-central Arizona, a distance of about 500·0 km (text-fig. 1). The northernmost locality (locality 1) is about 0·5 km east of the headquarters of Capitol Reef National Park in southern Utah. At this locality the leaf occurs in great numbers throughout a lens of brownish mudstone in the base of the Shinarump Member. The lens occupies a channel cut into the Moenkopi Formation (see text-fig. 3). Locality 1 has been assigned U.S. Geological Survey fossil plant locality number 10154.

Locality 2 is about 22 km south of locality 1 near the intersection of Oak Creek and Bear Canyons. In the vicinity of the intersection the Shinarump ranges from 0 to 6 m in thickness and occupies a north-eastward trending channel cut into the Moenkopi Formation (Smith *et al.* 1963). Here the member consists chiefly of sandstone and conglomerate but it also contains several discontinuous beds of carbonaceous shale and coaly material. The new *Eoginkgoites* occurs about 1 m above the Moenkopi in carbonaceous shale.

Locality 3 is about 10·0 km south of locality 2 and 0·8 km north-west of a butte called the Lamp Stand in the Circle Cliffs area of southern Utah. At this locality the new species occurs in the lower part of the Shinarump in a sequence of cross-bedded white to greyish sandstone and grey to greenish mudstone. The sequence occupies a channel about 9 m deep cut into the underlying Moenkopi Formation. The channel has been traced for a distance of about 100 km and is part of a pre-Shinarump drainage system that developed in the region during Late Triassic time (Davidson 1967, fig. 14). The new species is not very common at locality 3 and all specimens are fragmentary. This locality has been assigned U.S. Geological Survey fossil plant locality number 10153.

Locality 4 is about 23·0 km south of locality 3 and 0·8 km east of the point where Death Hollow Canyon crosses the Moenkopi Formation in the central part of the Circle Cliffs area. The new species occurs about 4·5 m above the Moenkopi Formation in coaly lenses and thin interbeds of mudstone in a bed of sandstone in the upper part of the Shinarump Member (text-fig. 3). Elsewhere in the Circle Cliffs area the bed overlies 30 m or more of white to grey sandstone which fills a deep stream channel cut into the Moenkopi Formation. According to Davidson (1967, fig. 14) this is the same channel that contains the new species at locality 3. In some layers the leaves of



TEXT-FIG. 3. Stratigraphic sections of the lower part of the Chinle Formation at some of the localities in Utah and Arizona that have yielded *Eoginkgoites davidsonii* sp. nov. The localities where the sections were measured are shown on text-fig. 1.

E. davidsonii sp. nov. are very densely packed. The locality has been assigned U.S. Geological Survey fossil plant locality number D1341.

Locality 5 is about 150 km east of locality 4 on the north side of The Notch, Elk Ridge, Utah (text-fig. 2). In this area the Shinarump Member ranges from 0 to about 9 m in thickness and consists mainly of cross-bedded sandstone. In places it also contains discontinuous lenses of mudstone that are often fossiliferous. At locality 5 the Shinarump occupies a broad, shallow, westward-trending channel cut into the underlying Moenkopi Formation. The channel is a part of the larger Elk Ridge–White Canyon channel system in which sediment was transported in a westerly direction from the ancient Uncompahgre highlands of western Colorado during Late Triassic time (Lewis and Campbell 1965). This locality has been assigned U.S. Geological Survey fossil plant locality number 9370.

Locality 6 is about 250 km south-west of locality 5 across the Little Colorado River from Cameron in north-central Arizona (text-fig. 1). The locality is in a lens of greenish grey mudstone which is about 2 m thick and 60 m wide. The base of the lens is about 3 m above the top of the Moenkopi Formation. The stratigraphic position of the lens is controversial. According to Cooley *et al.* (1969) it is in the Shinarump Member of the Chinle. Stewart *et al.* (1972) restrict the Shinarump to the beds of conglomerate and sandstone that directly underlie the lens and assign it to the sandstone and mudstone member of the Chinle. The presence in the lens of *Eoginkgoites* (which occurs only in the Shinarump elsewhere in the south-west) suggests that the lens should be included in the Shinarump as shown on text-figs. 2–3. Leaves are very abundant throughout the lens and frequently overlap each other. They are usually well preserved and the new *Eoginkgoites* is the most common leaf at the locality. This locality has been assigned U.S. Geological Survey fossil plant locality number 9377 and Museum of Northern Arizona locality number 197.

Locality 7 is the southernmost locality. It is about 250 km south-east of locality 6 and 8 km south-east of St. Johns, Arizona. At this locality the fossils occur in a lens of white to reddish claystone about 5 m thick and 750 m wide. The lens is separated from the Moenkopi by about 8 m of mottled strata. This locality has been assigned U.S. Geological Survey fossil plant locality number 9373.

SYSTEMATIC DESCRIPTIONS

Class BENNETTITALES

Genus *Eoginkgoites* Bock, 1952, emend. Ash, 1976

Generitype. Eoginkgoites sectoralis Bock, 1952.

Discussion. Three species of *Eoginkgoites* are now known. They are differentiated more or less arbitrarily on the basis of pinna proportions and size as shown below:

Key to the North American species of *Eoginkgoites*

1. Pinnae broad, length typically 2–4 × width (3–16 cm wide, 15–40 cm long) . . . . *E. davidsonii* sp. nov.
1. Pinnae narrow, length typically 5–8 × width 2
    2. Pinnae typically 5–15 mm broad, 25–90 mm long . . . . . *E. sectoralis* Bock
    2. Pinnae typically 40 mm broad, 180 mm long . . . . *E. gigantea* Bock

Bock's two species, *E. sectoralis* and *E. gigantea*, occur in the lower part of the Lockatong Formation of the Newark Group of Late Triassic age in Pennsylvania. *E. davidsonii* sp. nov. occurs in the basal strata of the Chinle Formation of Late Triassic age in Utah and Arizona.

Eoginkgoites has been recognized in the Upper Triassic Pekin Formation of the Newark Group in North Carolina (Hope, written communication, 1975). The specific identity of these fossils is unknown.

Eoginkgoites davidsonii Ash

Plates 77–79; text-figs. 4–6

1963 *Sphenozamites rogersianus* Fontaine ex Brown (in Smith *et al.* p. 16). Identification only.
1967 *Sphenozamites rogersianus* Fontaine ex Brown (in Davidson, p. 30). Identification only.
1972 *Sphenozamites rogersianus* Fontaine ex Brown (in Stewart *et al.* p. 85). Indentification only.

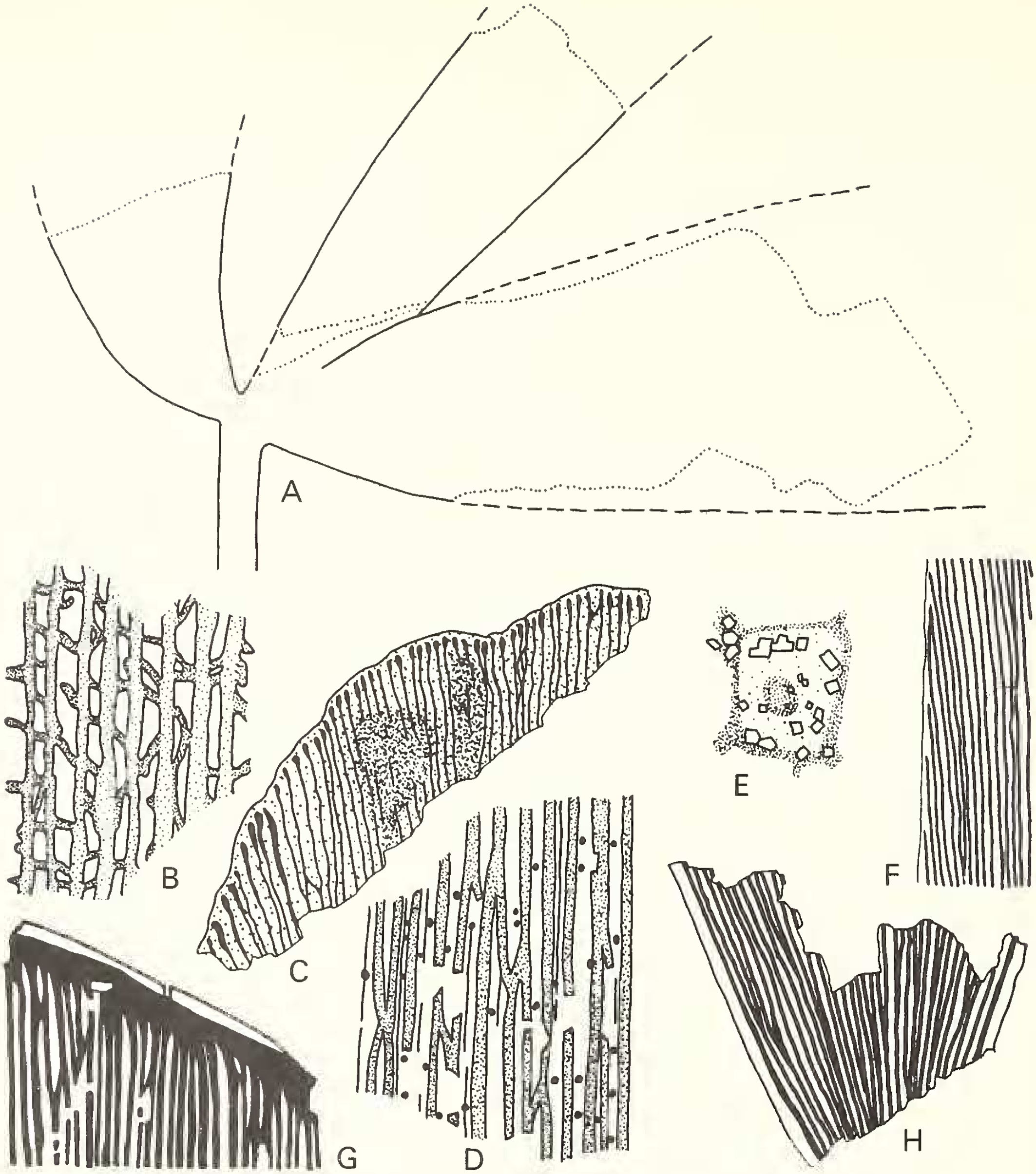
Holotype. USNM 172363. Paratypes: USNM 172357, 172359, 172360.

Derivation of name. The specific name honours Edward S. Davidson, of the U.S. Geological Survey who mapped the Circle Cliffs area in southern Utah and gave me much useful information on the localities there that subsequently yielded specimens of the species.

Diagnosis. Leaf pinnate, large, width known to reach 90 cm but sometimes as small as 20 cm wide, length unknown. Pinnae borne laterally and terminally on rachis, closely aggregated at upper end of rachis, apical pinnae usually fused at bases for about 2–4 cm, lateral pinnae free at bases. Pinnae wedge-shaped about equal in size on same leaf, widest near apex (largest 16 cm wide, 45 cm long, smallest 3 cm wide, 15 cm long). Lateral margins straight to slightly curved, without lobes, symmetrically contracted from widest point near apex to base. Apex nearly straight to rounded, occasionally wavy to slightly lobed but never showing sharp indentations or points. Lateral margins scarcely thickened below but gradually developing a thick rim above, apical margins with a strongly thickened rim formed by a marginal vein. Rachis robust, up to 12 mm wide, surfaces smooth and appearing similar, without a groove on the upper side.

Veins distinct, radiating from the base of each pinna, rather few and stout near base but forking and anastomosing frequently, in middle of pinna typically 0·1 mm broad, traversing lamina at a concentration of three to four per mm, most veins ending in a marginal vein but some meeting lateral margins and ending at a very acute angle with the margin. Free ends of veins often expanded. Dark rounded bodies about 150 μm × 100 μm, occurring at interval of about 0·5–1·0 mm, also occasional single longitudinal strands about 20 μm–30 μm wide occurring between veins.

Cuticle of lamina of medium thickness, about 3 μm above, 2 μm below (measured in folds). Details varying in different parts of leaf. Over most of pinna epidermal cells papillate but papillae becoming scarce to absent near pinna base. Upper cuticle generally showing uniform cells, veins not or scarcely indicated, cells tending to be rectangular, in longitudinal files, anticlinal walls strongly marked, essentially straight but always showing jagged and uneven thickenings, sculpturing on periclinal walls consisting of irregular, small thickened areas or low hollow papillae about 10 μm in diameter. Cells near base of pinnae irregularly arranged. Lower



TEXT-FIG. 4. *Eoginkgoites davidsonii* sp. nov. from the Shinarump Member of the Chinle Formation. A, apex of the rachis and the bases of three pinnae. Dotted lines represent the broken edges of the leaf and the dashed lines indicate the probable position of the pinnae margins. Holotype. USNM 172363, $\times\frac{1}{2}$. B, D, details of the venation. The dark transverse bars connecting the veins in B and the dark rounded bodies in D may be masses of resin or remnants of the fossilized mesophyll. USNM 222764, 222768, $\times 10$. C, apex of a pinna showing the wavy margin and the veins. Note that there is a large swelling at the end of each vein and that the marginal vein is absent. Some of the veins divide and join at several places in the fossil. USNM 222762, $\times 5$. E, a single cell showing pitting that frequently occurs on the cuticle of this species. USNM 172360b, $\times 400$. F, lateral margin of a pinna showing the veins which typically are free in this part of the leaf. USNM 222761, $\times 5$. G, apical region of a pinna showing the venation and the marginal vein which is well developed in this fossil. Some of the veins divide and join at several places in the fossil. USNM 222763, $\times 5$. H, basal region of a pinna showing the spreading veins that divide and join in places. USNM 172357, $\times 5$. Specimens in A, B, D, G, from locality 1 in Capitol Reef National Park, Utah; those in C, E, F, H from locality 4 near Death Hollow Wash in the Circle Cliffs, Utah.

cuticle showing veins distinctly, veins marked by several (usually three) files of elongated cells (20 μm–50 μm wide and long), anticlinal walls as on upper cuticle, periclinal walls strongly papillate, most papillae hollow, typically about 14 μm high, 10 μm in diameter. Some ordinary epidermal cells also bearing large sack-like papillae about 12 μm wide, 50 μm long.

Cuticle of petiole thick, about 5 μm, anticlinal walls of ordinary epidermal cells strongly marked on both upper and lower cuticles, side walls irregular to slightly wavy (up to 12 μm), end walls usually thick (up to 3 μm), straight, not irregular. Cells along sides of petiole irregularly arranged, in central region of petiole cells nearly uniform, arranged in longitudinal rows, square to rectangular or polygonal, end walls often arranged at 45° to side walls, periclinal walls smooth.

Stomata sparse (twenty to thirty per mm^2) on lower cuticle of lamina and petiole, rare (four to nine per mm^2) on upper cuticle, scattered or in irregular files between veins, mostly transverse to veins but some oblique or longitudinal particularly near and on petiole. Subsidiary cells rectangular, about the same size as normal epidermal cells, 18–32 μm long, 15–26 μm wide, each bearing a single, hollow, papilla. Papillae 10–16 μm long, 4–6 μm wide, usually overlapping adjacent guard cell and stoma. Guard cell dorsal cuticle thickened, about 4–6 μm wide, 25–30 μm long, two-thirds covered by subsidiary cell, slightly sunken at the bottom of a shallow rectangular epistomatal pit, lower surface marked with radially running striations about 0·5 μm broad. Poles of guard cells often overhung by neighbouring epidermal cells.

Description of material. This diagnosis is based on several dozen specimens. Most are fragmentary but a number of complete leaves have been observed in the field at locality 1. However, because of their large size and the nature of the matrix it has not been possible to collect an entire leaf from that locality. Estimates of the size of the leaf are based principally on specimens observed at locality 1.

Preservation varies considerably from locality to locality. At locality 2 most of the specimens are only carbon- and iron-stained impressions which give just the outline and venation of fossil. In many specimens from localities 1 and 7 the leaf substance has contracted into small bits of coaly material which yield tiny (1 mm or less) fragments of cuticle upon maceration. In other specimens the leaf is represented by a thin brownish residue. Transfer preparations of some of these specimens did give useful results. At locality 6 the fossil is represented by thin carbonaceous films which can be transferred. At locality 4 the cuticles are well preserved and often can be separated from the rock with a needle or small knife before maceration. Although these cuticles appear to be quite robust in the rock they do not tolerate more than 30 minutes in concentrated HNO_3 and $KCLO_3$.

In some of the fossils from locality 4 a thin layer of sediment has infiltrated between the upper and lower cuticles of the same leaf. In others there are rows of many low, narrow transverse ridges of brownish carbonaceous material adhering to the lower cuticle (Pl. 77, fig. 4). Possibly they are merely the plates observed in the transfer preparations of fossils from locality 6 (text-fig. 4B, D), or they may represent fossilized remnants of the mesophyll.

Pinna bases have not been found at locality 6 and they are rare at most other localities. The exception is at locality 1 where they occur quite frequently. Most of the pinna bases shown on Plates 77 and 78 are from this locality. At locality 7 some of the pinnae show evidence of fraying prior to burial. The fraying could have occurred while the leaves were still attached to the plant as in the living *Welwitschia* or after they fell and were being transported to the burial site. None of the leaves from the other localities shows this feature or any other type of damage.

No reproductive organ associated with *E. davidsonii* seems likely to belong to it. One locality (4) contains the fossil and nothing else. All the others contain several additional leaves although *E. davidsonii* is the most common fossil. There is nothing to unite the several large unidentified cones that occur with *E. davidsonii* at locality 1.

Discussion. The scanning electron photomicrograph of the stomata of this species in Plate 79, fig. 2 shows that the polar regions of the guard cells are partially divided longitudinally by a plate of cuticle. This observation tends to confirm Harris's (1932*a*, *b*) contention that the line he and others have observed in the same position on the stomata of several other bennettitaleans with light microscopes is a wall separating the guard cells. Such a line has been observed, for example, on the stomata of *Pterophyllum rosenkrantzi* Harris (1932*a*), *P. astartense* Harris (1932*b*), *P. compressum* Lundblad (1959), and *Ptilophyllum pecten* (Phillips) Harris (1969).

The striations noted on the lower surface of the dorsal guard cell cuticle of the new species are rather unusual (Pl. 79, fig. 2). These striations are visible with the light microscope (see text-fig. 4*d*) but it is impossible to determine their position. The scanning electron microscope showed their true position. Similar striations have been observed in only a few other Bennettitaleans such as *Williamsonia himas* Harris (1953) and *Pterophyllum zygotacticum* Harris (1932*b*).

Sac-like trichomes and medial papillae somewhat similar to those on the ordinary epidermal cells on the lower cuticle of the new *Eoginkgoites* occur on a second bennettitalean, *Zamites powelli*, that is found in the Chinle and other Upper Triassic units in North America (Ash 1975, text-fig. 4G). In addition they are similar to the trichomes found on *Otozamites penna* Harris (1969) from the Middle Jurassic of Yorkshire, *Pterophyllum zygotactium* Harris (1932*a*) from the Rhaetic of Greenland, and *P. filicoides* (Schlothelm) from the Carnian of Lunz, Austria (see Barnard 1970).

EXPLANATION OF PLATE 77

Figs. 1–9. *Eoginkgoites davidsonii* sp. nov. from the Shinarump Member of the Chinle Formation, Utah and Arizona. 1, apex of a pinna. The thickened rim formed by the marginal vein is darker than the rest of the pinna. Slide, USNM 172355, ×1. 2, bases of two pinnae, USNM 172366, ×½. 3, naturally macerated pinna in which the venation is visible, USNM 172356, ×½. 4, paratype, apex of the rachis and the base of several pinnae. The lower cuticle has been removed from the lamina and the upper part of the rachis. USNM 172360, ×1. 5, paratype, rachis and remains of a lateral pinna, USNM 172361, ×1. 6, apical region of the rachis and the remains of four pinnae, USNM 172358, ×½. 7, 8, slightly lobed apices of two pinnae, USNM 172365, ×½, USNM 172364, ×1. 9, remains of three pinnae, USNM 172359, ×½. Specimens in 1 and 8 from locality 6 near Cameron, Arizona; specimens in 2, 3, 6, 7, 9 from locality 1 in Capitol Reef National Park, Utah; specimen in 4 from locality 4 in the Circle Cliffs area, southern Utah; specimen in 5 from locality 7 near St. Johns, Arizona.

ASH, Triassic bennettitalean leaf

Small angular pits 2–12 μm in cross-section occur on the lower cuticle in the basal part of some pinnae of the new species (text-fig. 4E). Similar pits have been observed on the cuticle of the Chinle bennettitalean leaf *Nilssoniopteris* sp. nov. (Ash 1972), and on the cuticle of the Chinle conifer *Pagiophyllum* sp. C (Ash 1972). They have been observed also on the cuticles of other extinct conifers, such as *Stabbarpia* Florin (1958) and on the cuticles of certain living conifers including *Sequoiadendron giganteum* (see Florin 1931). Such pits have been attributed to calcium oxalate crystals embedded in the outer walls of the epidermal cells of these leaves by Florin (1958, p. 310). The pits do compare favourably in size and shape with calcium oxalate crystals that I have obtained by evaporating a solution of calcium oxalate dissolved in dilute hydrochloric acid.

In one specimen of the new species from locality 1 the petiole is represented by a limonite-stained cast about 3 cm long, 4 mm thick, and 8 cm wide. The surface of the cast is covered with a thin layer of carbon. Several thin irregular layers of carbon occur also within the core and form an irregular oval as shown in text-fig. 5H–J. Probably at least some of these layers represent the crushed vascular tissue of the petiole. There is no evidence of a medial groove or of two vascular bundles in the cast as reported in the petiole of *E. gigantea* by Bock (1969). In fact the carbonaceous layers seem to match the arrangement of vascular tissue reported in *Monathesia* and other petrified cycadeoid stems (see Delevoryas 1959).

Comparisons. As noted earlier the leaf described here can be separated from the other species of the genus *Eoginkgoites* by the proportions of the pinnae. What are taken to be typical pinnae of *E. davidsonii* sp. nov. are much longer and wider than the pinnae of both *E. sectoralis* and *E. gigantea* and they should not be confused. Small pinnae of *E. davidsonii* sp. nov., however, may cause confusion as they are about the same length as the pinnae of *E. gigantea.* Generally the small pinnae of the new species are much wider than the pinnae of the other species and thus are easily distinguished. Regretfully nothing is known about the cuticle of the *E. sectoralis* and *E. gigantea* so additional comparisons are limited.

The leaf called *E. davidsonii* sp. nov. can be easily distinguished from *Sphenozamites rogersianus* Fontaine (1883) the species with which it was confused by Brown (see synonymy). The basic architecture of the two leaves is very different. In *S. rogersianus*,

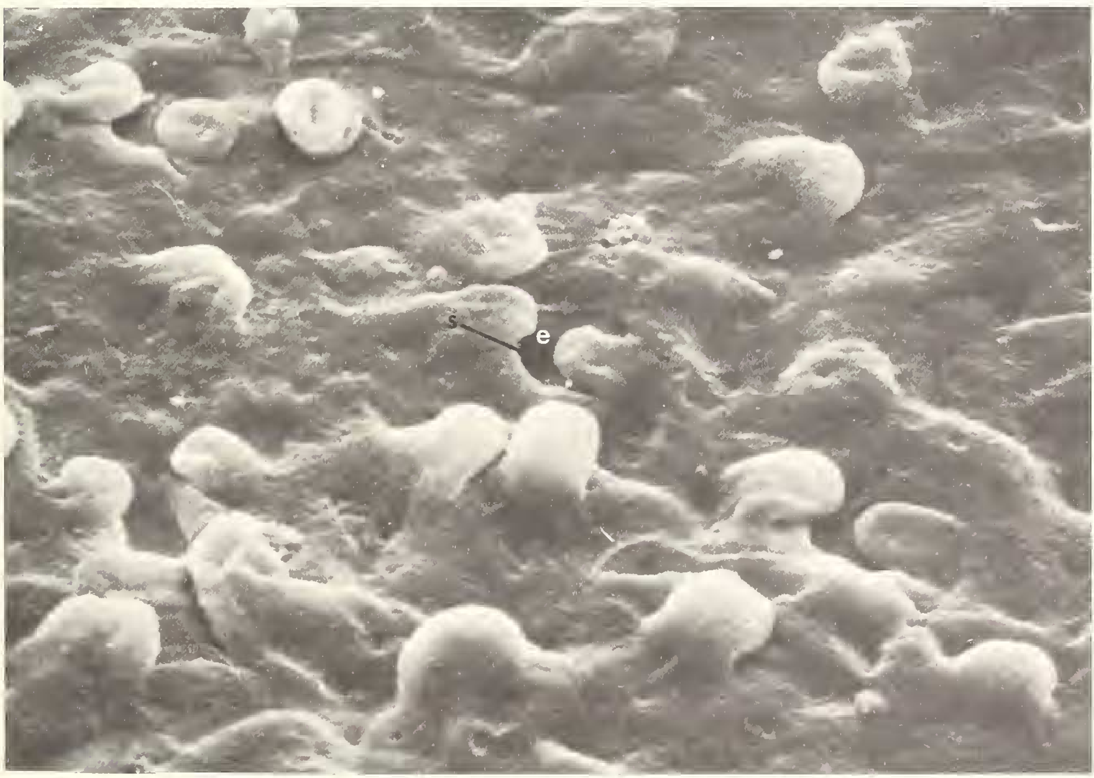
---

EXPLANATION OF PLATE 78

Figs. 1–3. Scanning electron photomicrographs of the outer surface of the lower cuticle of *Eoginkgoites davidsonii* sp. nov. 1, papilla on an ordinary epidermal cell of the lamina. Many small wrinkles and pits are visible on both the papilla and adjacent surfaces, ×4000. 2, 3, stomatal apparatuses and subsidiary cell and ordinary epidermal cell papillae. Note the rectangular epistomatal chambers at several places in the figures. The outer surface of the dorsal guard-cell cuticles form the floors of chambers. Several of the papillae shown in the upper part of fig. 3 have collapsed giving them the appearance of doughnuts. 2, ×1200; 3, ×1000. Material from the Shinarump Member of the Chinle Formation at locality 4 in the Circle Cliffs area, southern Utah.

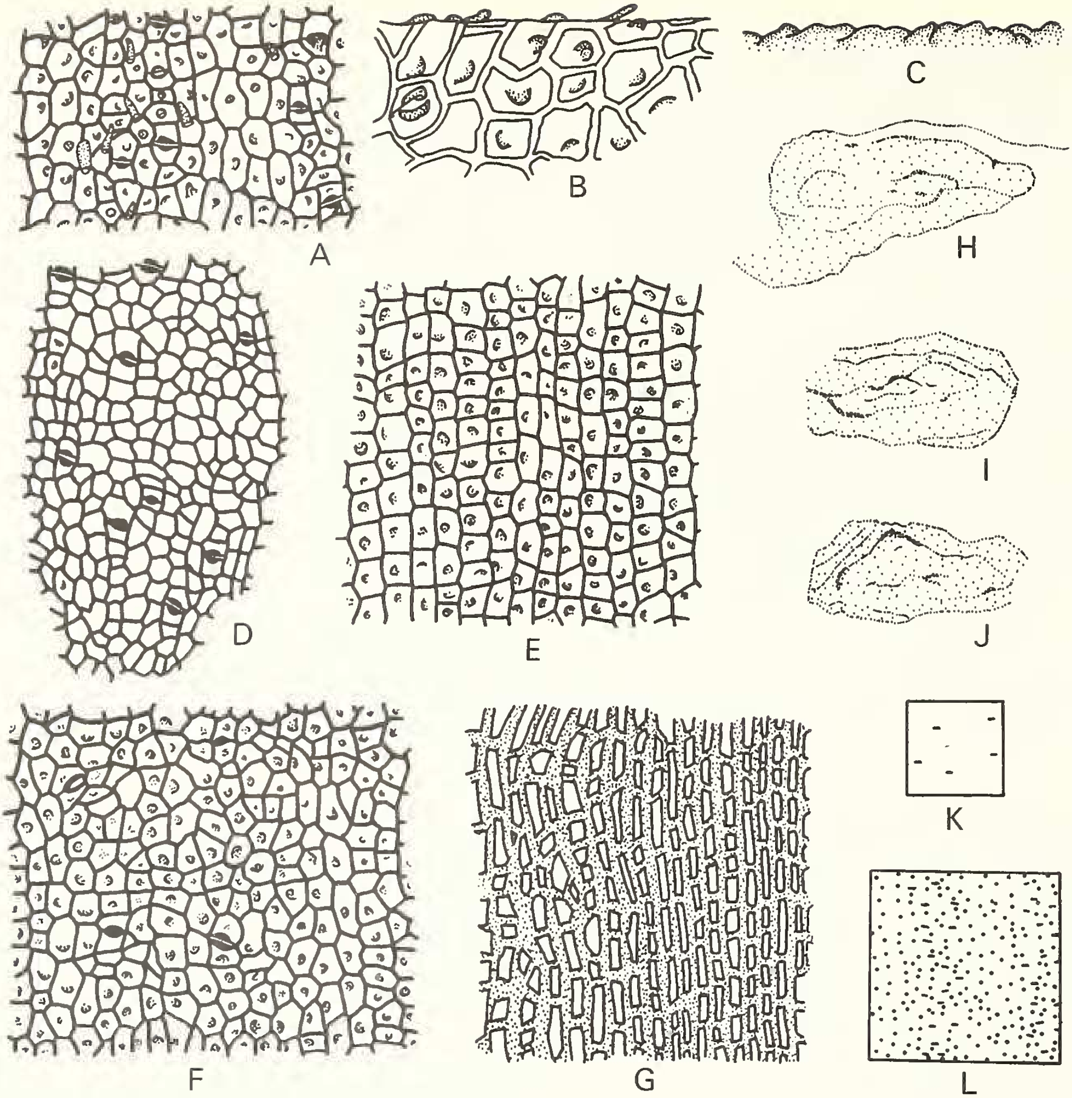
1

2



3

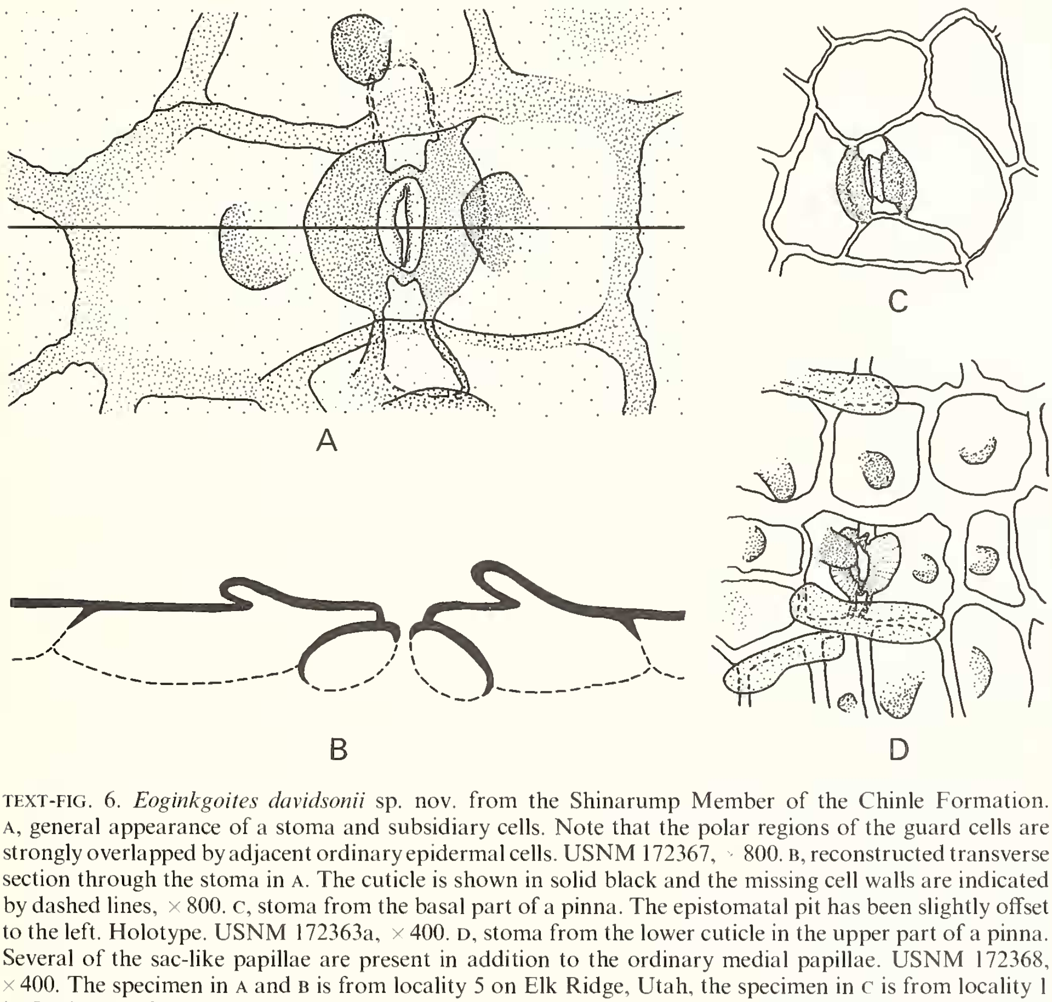
ASH, Triassic bennettitalean leaf



TEXT-FIG. 5. *Eoginkgoites davidsonii* sp. nov. from the Shinarump Member of the Chinle Formation. A, lower cuticle of lamina in the upper part of a pinna showing two stomatiferous zones. Note that each of the epidermal cells shows a medial papillae as is typical of the cells in this part of the leaf. Several of the large sac-like papillae are also present. Compare with D. USNM 172368, ×100. B, fold in the cuticle of the lamina showing the medial papillae. USNM 172362, ×200. C, papillae along the edge of the apex of a pinnae. USNM 222766, ×200. D, upper cuticle of the lamina in the basal part of a pinna. As indicated in the figure the outer surfaces of the epidermal cells are typically smooth and non-papillate in the basal part of the pinnae of this species. Compare with A. USNM 172360a, ×100. E, upper cuticle of the lamina in the upper part of a pinna showing papillate epidermal cells as is characteristic of this part of the leaf. Note the absence of stomata. USNM 172362, ×100. F, lower cuticle of the lamina a short distance above the basal region of a pinna. In this part of the leaf the epidermal cells are more irregular than higher up and the stomatiferous zones and non-stomatiferous zones are not as well defined. Compare with A. USNM 172360a, ×100. G, cuticle from the petiole showing elongate thick-walled epidermal cells. USNM 222765, ×100. H–J, cross-sections of the petiole. The carbonaceous material in the sections is indicated by dots. USNM 222767A, B, ×5. K, distribution and orientation of stomata (short lines) in 1 sq mm of the petiole cuticle. USNM 222765, ×25. L, distribution and orientation of stomata (short lines) and of papillae (dots) on 1 sq mm of the lower cuticle of the lamina a short distance above the basal region of a pinna. USNM 172362, ×50. Specimens in A, H–J from locality 1 in Capitol Reef National Park, Utah; those in B–G, K, L from locality 4 near Death Hollow Wash in the Circle Cliffs area, Utah.

which for no clear reason was transferred by Bock to the genus *Glandulozamites*, the pinnae are arranged laterally on a long rachis whereas in the new species the pinnae are arranged at the end and along the margins of a very short rachis. In *S. rogersianus* there are typically two or three pinnae with fused bases at the end of the rachis but only one in the new species. The pinnae also show significant differences. In *S. rogersianus* the pinnae are obovate to rectangular and in the new species they are wedge-shaped. The venation is free dichotomous in *S. rogersianus* whereas it is anastomosing in *E. davidsonii*.

Pinnae of the new *Eoginkgoites* are somewhat like certain species of the Permian-Triassic genus *Noeggerathiopsis* Feistmantel (see Maithy 1965) and the poorly known Triassic genus *Chiropteris* Kurr (in Bronn 1858). *Noeggerathiopsis* and *Chiropteris* are simple leaves consisting of an ovate to spathulate blade which usually has a broadly



TEXT-FIG. 6. *Eoginkgoites davidsonii* sp. nov. from the Shinarump Member of the Chinle Formation. A, general appearance of a stoma and subsidiary cells. Note that the polar regions of the guard cells are strongly overlapped by adjacent ordinary epidermal cells. USNM 172367, × 800. B, reconstructed transverse section through the stoma in A. The cuticle is shown in solid black and the missing cell walls are indicated by dashed lines, × 800. C, stoma from the basal part of a pinna. The epistomatal pit has been slightly offset to the left. Holotype. USNM 172363a, × 400. D, stoma from the lower cuticle in the upper part of a pinna. Several of the sac-like papillae are present in addition to the ordinary medial papillae. USNM 172368, × 400. The specimen in A and B is from locality 5 on Elk Ridge, Utah, the specimen in C is from locality 1 in Capitol Reef National Park, Utah, and the specimen in D is from locality 4 near Death Hollow Wash in the Circle Cliffs area, Utah.

rounded apex and sides that taper evenly to a narrow base. None of the species of those two genera, however, has lateral pinnae below a terminal pinna as in *E. davidsonii* sp. nov. Also the pinnae of the new species are usually larger than either *Noeggerathiopsis* and *Chiropteris*. The venation is free dichotomous in *Noeggerathiopsis* whereas it is anastomosing in *E. davidsonii* sp. nov. and there is a ring of subsidiary cells around the guard cell pair in *Noeggerathiopsis* (one subsidiary cell opposite each guard cell in the new species). The venation of *Chiropteris* and the new species is anastomosing and remarkably similar. However, the cuticle of *Chiropteris* is unknown and the fossil is often classified as a fern.

Comments. As noted above, *E. davidsonii* sp. nov. occurs only in the basal strata of the Chinle Formation in the Shinarump Member. It does not occur in the large floras known from higher Chinle strata at Fort Wingate, New Mexico (Ash 1970*a*, 1972), in Petrified Forest National Park, Arizona (Daugherty 1941; Ash 1972), in Capitol Reef National Park, Utah, or near St. Johns, Arizona. The relative stratigraphic position of these localities is shown on text-fig. 2. Also the species has not been recognized in any of the several dozen smaller floras known from the Chinle elsewhere in the South-west (Ash 1972; Stewart *et al.* 1972) or in any other formation. The limited distribution of *E. davidsonii* sp. nov. suggests that it was narrowly restricted both geographically and stratigraphically. Undoubtedly this is due at least in part, to the incompleteness of the fossil record but, nevertheless, it appears that the new species may be a guide fossil to the lowermost part of the Chinle Formation.

Probably *E. davidsonii* sp. nov. lived in a very moist environment in or adjacent to swampy areas. It is most abundant at localities 1, 4, and 5 where it is densely packed in thin lenses that have a limited lateral extent. These lenses appear to have accumulated in swamps or a paludal environment of some sort. They consist of dark mudstone that contains fern leaves and many other plant fossils and much organic matter. In addition the stems of *Equisetites* occur in the position of growth in one of these lenses at locality 1 in Utah. The new species appears to have been a dominant in the Upper Triassic environments represented by the deposits.

Eoginkgoites is uncommon at the other localities in the South-west and most of the specimens are fragmentary. Some are frayed as if they had been transported some

---

EXPLANATION OF PLATE 79

Figs. 1–2. Scanning electron photomicrographs of the cuticle of *Eoginkgoites davidsonii* sp. nov. 1, general view of a stomatal apparatus and vicinity. A second stomatal apparatus is in the upper-left corner of the figure. Openings into ordinary epidermal and subsidiary cell papillae are visible at several places. Note the irregular anticlinal flanges of the subsidiary and ordinary epidermal cells, ×2800. 2, stomatal apparatus seen from the inside of the cuticle showing prominent radiating striations on the guard-cell's cuticle. The area of overlap of the polar regions of the guard cells by adjacent ordinary epidermal cells is visible in this figure. The wall separating the guard cells in the polar regions is at *w*. Note that the anticlinal flanges of the subsidiary and ordinary epidermal cells are rather irregular. Compression of the thin cuticle of the free edge of the dorsal guard-cell cuticle has formed a thickened rim. Compare this figure with the diagram of a bennittitalean stomata given by Harris (1932, fig. 37H), ×3000. Material from the Shinarump Member of the Chinle Formation at locality 4 in the Circle Cliffs area, southern Utah.

1

2

ASH, Triassic bennettitalean leaf

distance. Only a few other plant fossils occur at these localities and they too are fragmentary. The containing rock at these localities is light coloured shale or sandstone which does not contain much organic matter. The sandstone beds often show cross-bedding and other features characteristic of stream deposits. Possibly *Eoginkgoites* lived in the swampy margins of Upper Triassic streams and its remains fell into the moving water together with other plants and they were generally fragmented before burial.

Certain features of *E. davidsonii* sp. nov. suggest that the plant grew in a warm, moist environment and substantiate the theory that it inhabited a paludal environment. This is especially obvious if *E. davidsonii* sp. nov. is compared with the Jurassic plants of Yorkshire which are thought to have grown in a moist tropical climate (Seward 1933). These features include:

1. A relatively thin cuticle (often thick in the Jurassic plants of Yorkshire).
2. Some stomata on upper side of leaf (nearly always limited to the lower cuticle of the Yorkshire Jurassic plants).
3. Individual stomata only slightly sunken and stomatal surface not in grooves (mostly sunken and often in grooves in the Jurassic plants of Yorkshire).
4. Subsidiary cell papillae small and rarely covering aperture (subsidiary cell papillae often large and covering aperture in the Jurassic plants of Yorkshire).
5. Broad, rather thin lamina (frequently contracted and thick in the Jurassic plants of Yorkshire).

Acknowledgements. I am grateful to Professor T. M. Harris and Dr. Peter Barnard, University of Reading, for their comments about this report. Also I acknowledge with thanks the assistance of Arthur H. Watt, Washington, D.C. who loaned specimens of this species to me from the stratigraphic collections of the U.S. Geological Survey, the assistance of Marianne Abel, Philadelphia, Pennsylvania, who loaned me specimens of *E. sectoralis* from the collections of the Academy of Science, and the help of E. S. Davidson, Tucson, Arizona, who directed me to some fossil plant localities in the Circle Cliffs area, Utah. I thank the Superintendent, Capitol Reef National Park, Utah, for allowing me to collect from areas under his supervision. Research supported by the Earth Sciences Section, National Science Foundation, Grant GA-25620.

The fossils described here have been deposited in the U.S. National Museum (USNM), Washington, D.C.

REFERENCES

ASH, S. R. 1970*a*. Ferns from the Chinle Formation (Upper Triassic) in the Fort Wingate area, New Mexico. *Prof. Pap. U.S. Geol. Surv.* **613**-D, D1–D52, 5 pls., 19 figs.

—— 1970*b*. *Dinophyton*, a problematical new plant genus from the Upper Triassic of the southwestern United States. *Palaeontology*, **13**, 646–663, pls. 122–124, 6 figs.

—— 1972. Plant Megafossils of the Chinle Formation. *In* BREED, C. S. and W. J. (eds.). *Investigations of the Chinle Formation. Bull. Mus. Northern Ariz.* **47**, 23–43, 1 pl., 4 figs.

—— 1975*a*. *Zamites powelli* and its distribution in North America. *Palaeontographica*, **149** (B), 139–152, 2 pls., 5 text-figs.

—— 1975*b*. The Chinle (Upper Triassic) flora of southeastern Utah. *Four Corners Geol. Soc. Guidebook, 8th Field Conf., Canyonlands*, 143–147, 6 figs.

—— 1976. The systematic position of *Eoginkgoites*. *Am. J. Bot.* **63.**

BARNARD, P. D. W. 1970. Upper Triassic plants from the Kalawch River, North-east Afghanistan. In *Italian Exped. Karkorum* (K^2) *and Hindu Kush, Sci. Repts.* Pt. 4, 2, pp. 25–40, pls. 4–5, 3 figs.

BOCK, W. 1952. New eastern Triassic ginkgos. *Bull. Wagner Free Inst. Sci.* **27,** 9–14, 1 pl.

—— 1969. The American Triassic flora and global distribution. *Geol. Cen. Res. Ser.* **3** and **4**, 406 pp., 639 figs.

BREED, C. S. and W. J. (eds.) 1972. *Investigations in the Triassic Chinle Formation. Bull. Mus. Northern Ariz.* **47,** 103 pp.

BRONN, J. G. 1858. Beitrage zur triassischen Fauna und Flora der bituminosen Schiefer von Raibl. *Neues Jahrb. Min., Geol., Paläo.* 1–32, 129–144, pls. 1–12.

BROWN, R. 1956. Palmlike plants from the Dolores Formation (Triassic) southwestern Colorado. *Prof. Pap. U.S. Geol. Survey*, **274**-H, 205–209, pls. 32–33.

COOLEY, M. E., HARSHBARGER, J. W., AKERS, J. P., HARDT, W. F. and HICKS, O. N. 1969. Regional hydrogeology of the Navajo and Hopi Indian reservations, Arizona, New Mexico and Utah. Ibid. **521**-A, A-1–A-61, 5 pls., 20 figs., 8 tables.

DAUGHERTY, L. H. 1941. The Upper Triassic flora of Arizona *with* discussion of its geologic occurrence by H. R. Stagner. *Carnegie Inst. Washington Pub.* **526,** 108 pp., 34 pls.

DAVIDSON, E. S. 1967. Geology of the Circle Cliffs area, Garfield and Kane Counties, Utah. *Bull. U.S. Geol. Survey*, **1229,** 140 pp., 2 pls., 20 figs., 7 tables.

DELEVORYAS, T. 1959. Investigations of North American Cycadeoids: *Monanthesia. Amer. J. Bot.* **46,** pp. 657–666, 23 figs.

DORF, E. 1958. The geologic distribution of the Ginkgo family. *Bull. Wagner Free Inst. Sci.* **33,** pp. 1–8, 3 figs.

FLORIN, R. 1931. Untersuchungen zur stammesgeschichte der coniferales und Cordiatales. *Kgl. Svenska vetenskapsakad handlingar*, Ser. 3, **10** (1), 588 pp., 57 pls.

—— 1958. On Jurassic taxids and conifers from northwestern Europe and eastern Greenland. *Acta Horti Bergiani*, **17** (10), 257–402, pls. 1–56.

FONTAINE, W. M. 1883. Contribution to the knowledge of the older Mesozoic flora of Virginia. *U.S. Geol. Survey Mon.* **6,** 144 pp., 54 pls.

GREGORY, H. E. 1916. The Navajo country, a geolgraphic and hydrologic reconnaissance of parts of Arizona, New Mexico, and Utah. *U.S. Geol. Survey Water Supply Paper*, **380,** 219 pp.

HARRIS, T. M. 1932*a*. The fossil flora of Scoresby Sound, east Greenland, Part 2. *Medd. om Gronland*, **85** (3), 114 pp., 9 pls., 39 figs.

—— 1932*b*. The fossil flora of Scoresby Sound, east Greenland, Part 3. Ibid. **85** (5), 130 pp., 19 pls., 52 figs.

—— 1953. Notes on the Jurassic flora of Yorkshire, 58–60. *Ann. Mag. nat. Hist.* Ser. 12, **6,** 33–52, 6 figs.

—— 1969. *The Yorkshire Jurassic flora, III, Bennettitales.* Brit. Mus. (Nat. Hist.), 186 pp., 7 pls., 69 figs.

KRAUSEL, R. 1949. Koniferen und andere Gymnospermen aus der Trias von Lunz, Nieder-Osterreich. *Palaeontographica*, B, **89,** pp. 35–82, pls. 6–18, 18 text-figs.

—— and SCHAARSCHMIDT, F. 1966. Die Keuperflora von Neuewelt bei Basel. IV. Pterophyllen und Taeniopteriden. *Schweizerische Paläont. Abh.* **84,** 1–64, pls. 1–15, figs. 1–11.

LEWIS, R. Q. and CAMPBELL, R. H. 1965. Geology and uranium deposits of Elk Ridge and vicinity, San Juan County, Utah. *Prof. Pap. U.S. Geol. Survey*, **474**-B, 69 pp., 2 pls., 33 figs., 4 tables.

LUNDBLAD, A. B. 1959. Studies in the Rhaeto-Liassic floras of Sweden, II: 1, Ginkgophyta from the mining district of northwest Scania. *Kgl. Svenska vetenskapsakad handlingar*, Ser. 4, **6** (2), 38 pp., 6 pls., 9 figs.

MAITHY, P. K. 1965. Studies in the *Glossopteris* flora of India—20. *Noeggerathiopsis* and allied remains from the Karharbari Beds, Giridih Coalfield, India. *Paleobotanist*, **13,** pp. 94–100, 1 pl.

SCOTT, R. A. 1960. Pollen of *Ephedra* from the Chinle Formation (Upper Triassic) and the genus *Equisetosporites. Micropaleontology*, **6,** pp. 271–276, 1 pl., 2 figs.

SEWARD, A. C. 1933. *Plant life through the ages.* Cambridge Univ. Press, 603 pp., 139 figs.

SMITH, J. F. Jun., HUFF, L. D., HINRICHS, E. N. and LUEDKE, R. G. 1963. Geology of the Capitol Reef area, Wayne and Garfield Counties, Utah. *Prof. Pap. U.S. Geol. Survey*, **363,** 102 pp., 2 pls., 33 figs.

STEWART, J. H., POOLE, F. G., WILSON, R. F., CADIGAN, R. A., THORDARSON, W., ALBEE, H. F. 1972. Stratigraphy and origin of the Chinle Formation and related Upper Triassic strata in the Colorado Plateau region. Ibid. **690,** 336 pp., 5 pls., 34 figs.

S. R. ASH

Department of Geology
Weber State College
Ogden
Utah, 84404
U.S.A.

Typescript received 9 March 1976
Revised typescript received 1 September 1976

M